THE MOVEMENTS OF THE ENTEROPNEUSTA AND THE MECHANISM BY WHICH THEY ARE ACCOMPLISHED.

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The observations upon which the present paper is based were made, so far as they pertain to the living animal, upon two species of the group found on the Coast of California and Washington. These are *Balanoglossus occidentalis* Ritter (MS.) and *Delichoglossus pusillus* Ritter (MS.). The first mentioned is abundant at Puget Sound, and is found, though in small numbers, at San Pedro, California. The second is widely distributed along the Coast of California and is exceedingly abundant at San Pedro, where it lives side by side with the first.

My study of the movements have been made mostly on *D. pusillus*. This small species is so abundant in limited areas at San Pedro that a single shovelful of the sand in which it lives may contain several dozen. Its place of greatest abundance is a large sand flat, exposed at low tide, just inside the mouth of the inner harbor at Timm's Point. The sand in which the animals live is compact and homogeneous and contains much fine argillaceous material, the whole being blackened by decaying organic matter. In some places the creature is found among the roots of scattered patches of eel grass. Although the species is closely related to *D. Kowalevskii* of the Atlantic Coast of the United States, it is considerably smaller. It never produces the coiled castings so characteristic of its eastern relative. In fact, I have failed to discover any marking on the surface of the sand that can be relied upon to reveal the presence of the creature. The absence of the casts which are such a convenience to the collector is, however, compensated by the animal's habit of the protrusion of the proboscis from the ground. At low tide large numbers of the orange-colored proboscises may be seen with the tips only, or sometimes with nearly the entire organ, lying flaccid on the sand. A slight jarring of the ground causes a prompt withdrawal of the exposed part. Professor B. M. Davis, of the Los Angeles State

Normal School, first called my attention to the fact that the protrusion of the proboscis occurs only while the sand is uncovered during low tide; that withdrawal takes place almost immediately upon the incoming of the tide. My own observations confirm this. I have several times searched the ground in which the animals are abundant, when it was covered by a few inches only of still, clear water, and have never under such conditions seen a single extruded proboscis. The meaning of this habit is not clear.

Movements of both boring and locomotion are effected in the enteropneust through a combination of ciliary and muscular action. When crawling about on the surface of objects, which it does with considerable facility, the ciliary method is chiefly, though by no means exclusively, depended upon. When boring, or moving up and down its canal, muscular action is on the other hand most used.

The best way to observe the movements is to allow the animals to bury themselves in sand contained in a glass vessel. Under such circumstances they are certain to move along the inner surface of the glass if the vessel be small (a test-tube or homeopathic vial, for example, I have found favorable), for a portion of the time, and the whole operation may then be easily watched.

By far the most vigorous activity in any portion of the animal, both ciliary and muscular, goes on in the proboscis. The ciliary action is seen to best advantage when the animal is moving about on a sandy surface on which there are small elevations with which the tip of the proboscis comes in contact now and then; for the creature does not readily bring its proboscis tip into contact with a perfectly even surface on which it may rest. As the end of the proboscis touches the slope of a sand hillock, a perfect flood of sand grains is at once started which soon wholly encircles the organ and passes rapidly back to the collar. Arrived here the rapidity of the flow is greatly lessened so that if the picking up of grains at the tip be prevented a girdle of sand is soon formed around the collar.

If, on the other hand, the acquisition of grains be not interrupted the whole proboscis and collar become coated by a continuous sheath of sand which gradually extends backward until

the whole animal is covered, the sheath being scarcely more than one or two grains in thickness. The backward movement of the sand on the collar and body is effected chiefly by the pushing force of the ciliary action of the proboscis, though a weak ciliary action on the collar and thorax also contributes to the result, as does likewise muscular contractions of the proboscis. The prolific secretion of mucus particularly by the proboscis and collar serves to agglutinate the sand grains, to produce the sheath above mentioned. This sheath forms a well-defined tube when produced under the conditions here described so firm as to support itself in pieces of considerable size when pulled off and held up in the water.

Simultaneously with the ciliary action the animal is undergoing almost constant contortions through muscular action; but the true nature and significance of the motions of this kind are not seen until the creature is observed in the processes of burrowing. Here the meaning of a characteristic movement of the proboscis which is constantly noticed when the animal is not buried is readily seen. I refer to the contraction waves that move along the organ from tip to base, but which often remain stationary in the form of great blebs.

When in its burrow these blebs act chiefly as hold-fasts by which, through the contraction of the longitudinal muscles of the proboscis and collar, the whole body is drawn forward. The muscles most concerned in this are first those of the proboscis; second, the radio-longitudinal muscles of the collar; and third, the longitudinal muscles of the thorax-abdomen.

The proboscis tip is driven forward in making a new burrow partly by the action of the cilia, and partly by the contraction of the layer of circular muscle fibers, the former apparently playing the more important part.

The wave motion so characteristic of the proboscis does not appear on the collar, thorax, or abdomen, so that it plays no part in the advancement of these portions of the body. The collar shortens and elongates without great change in diameter, though the anterior rim is sometimes narrowed down considerably, the possible change in length of the part being nearly or quite one half its entire length in the fully extended state. The shortening is un-

doubtedly effected almost wholly by the contraction of the radio-longitudinal muscles. The extension is probably accomplished, as Spengel believes, by the inflation of the collar cœlom with water through the collar funnels.

Observation on the movements of the animal furnishes little satisfaction to one's quest after a reason for the existence of the peduncle that joins the proboscis and collar. At the same time, however, such observation does emphasize the importance of the slender isthmus's being both strongly constructed in itself and also firmly anchored at the ends to the larger parts of the body into which they are inserted. As the animal draws its long body about by its proboscis, it frequently looks as though the slender peduncle would be pulled out by the roots, particularly at its collar end. One naturally conjectures that the existence of the peduncle is to increase mobility at this particular place, and this perhaps is its significance, though it is not clear that the peduncle is in reality more flexible than the proboscis, especially when the latter is perfectly flaccid, for I have seen this part when the animal was in its canal double back upon itself so as to bring the two limbs into contact throughout their length, the tip of the organ being carried back to its base. The collar and thoracic portions of the body, however, are always, and the proboscis when muscular contractions are in progress, relatively rigid; and it is probably under these conditions that the mobility assured by the peduncle, finds its importance.

Having now the facts before us relative to the movements of the animal, we may consider the anatomical structures upon which these depend.

The proboscis possesses a typical dermo-muscular tube and its movements are essentially of the wave form usual to this type of musculature. The close resemblance between the movements of the enteropneust proboscis and those of the nemertean may be especially mentioned.

The thorax-abdomen, also, may be regarded as possessing the dermo-muscular tube, though here circular muscles are either altogether wanting or are very imperfectly developed, so that the wave movement does not here take place. Furthermore the longitudinal muscles are much stronger in the ventral than in the

dorsal half of the body in these regions. Ventral curvature as well as fore-and-aft shortening is consequently a general result of the contraction of these muscles.

The chief interest in the myology of the animal centers in the collar and peduncle. Here we have no dermo-muscular tube, but, on the contrary, a musculature of a fundamentally different type. The muscles, both longitudinal and circular, of the dermo-muscular tube are always, it will be recalled, strictly somatic, *i. e.*, they belong to the *body wall.* The chief mass of muscles of the collar and peduncle, viz., the radio-longitudinal muscles, while attached to the body wall at one end, at the other are on the other hand attached to the *notochord* and *nuchal skeleton* mainly, but partly also to the *wall of the esophagus.*

The full details of the origin, insertion, and relations of these large muscles are too complicated to admit of being fully set forth otherwise than by an elaborate, well-illustrated description; but an understanding of the most important facts may be given by a brief presentation, particularly if reference be made to Spengel's monograph. Figures 11, Pl. 14, and 20, 28, 32 and 34, Pl. 15, *lmi.* marking the muscles under consideration, are especially clear and instructive in this connection.

The two muscle masses are bilaterally situated and are in general coextensive in length with the collar and peduncle together. Their origins are on the sides of the combined notochord and nuchal skeleton anteriorly, *i. e.*, in the peduncle; and on the esophageal notochord and esophagus itself posteriorly, *i. e.*, in the collar (compare Figs. 4 and 7, *i. l. c. m.*, Pl. VII., of the author's paper on *Harrimania maculosa*[1]).

From these extensive origins the fibers extend backwards and outwards, some to become inserted into the outer edges of the septum separating the thoracic and collar cœloms; some, with a more oblique course, to insert into the ectoderm or the underlying connective tissue, along the postero-lateral portions of the collar; and still others at the anterior end of the collar, with a course predominantly radial, to insert into the ectoderm of the

[1] Papers from the Harriman Alaska Expedition, II. *Harrimania maculosa*, a new genus and species, etc. *Proc. Wash. Acad. of Sciences*, Vol. II., Aug. 20, 1900, p. 111.

anterior rim of the collar. By the contraction of these muscles when the proboscis acts as a fixed point through the pressure of the blebs above described against the sides of the burrow, the collar and, of course, the whole pharyngeal-abdominal portion of the body, are drawn strongly forward. Following, or coincidently with, this movement, contraction of the longitudinal muscles of the last-mentioned parts themselves takes place which contributes still further to the advancement of the creature as a whole. Circular somatic muscles are practically wholly wanting in the collar. A few fibers have been described in some species, but I am unable to recognize any excepting a few in the anterior rim, in any of the species examined by me.

From the account here given it is seen that we have in these animals *a system of locomotor muscles acting on an axial skeleton, derived in large part from the digestive tract.* That the combined notochord, consisting of the proboscis and esophageal portions, and nuchal skeleton, must be interpreted as a *unit of structure with the office of an axial skeleton*, I hope to be able to show conclusively in my forthcoming monograph of the Enteropneusta of the Pacific Coast. I imagine, however, that the proposition will be readily granted by most zoölogists, particularly if the facts here briefly set forth be considered along with others that may be gathered from previous publications on the anatomy and development of these animals.

If now the considerations relative to the skeleton and muscles be regarded from the comparative standpoint, the most striking thing that comes to view is the trenchancy with which they separate the enteropneusta from all the invertebrata. Nowhere in all the variety of organization represented by this subkingdom do we find locomotion accomplished by *muscles attached either to the intestinal tract or to derivatives of it.* But the trenchancy with which the structural relations here considered separate the enteropneusta from the invertebrata is no greater than that by which they connect them with the chordata.

An axial skeleton derived primarily from the intestinal tract and serving as the attachment of muscles of locomotion is, as is fully recognized, one of the very essences of chordate organization; and in spite of the difficulties in the way of establishing a

complete homology point by point between the axial skeleton (as I have defined it) of the enteropneust with its appended radio-longitudinal muscles of the collar, and the axial skeleton of amphioxus with its attached system of muscle plates, I can but believe that the two systems must have had, far back, a common origin.

But the problem is too large to admit of extended discussion in the present communication. My immediate purpose will have been attained if I shall have called the attention of zoölogists to the undoubted fact, as it seems to me, that the *muscular relations in the collar region of the enteropneusta must receive consideration from a point of view that has not hitherto been held, in all future attempts to elucidate the kinships of this group of creatures.*

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